CHARACTERISTIC EXAMPLES OF ACCUMULATIVE PROGRESSIVE EVOLUTIONARY MOVEMENTS.*

STUDIES IN DETERMINATE EVOLUTION, V.

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The proper way to study evolutionary movements is to follow out the changes which occur in the activity of particular potentialities, and it is evident that a proper phyletic taxonomy can result only when the entire complex of hereditary potentialities possessed by the cell and expressed as characters in the individual is taken into consideration. Furthermore, the addition of potentialities step by step in a definite progression is one of the very striking manifestations of the evolutionary process by which comparative levels may be determined. In the present paper, studies of five prominent series of this nature are outlined. The first four deal with progressions within rather narrow limits and are confined in each case to a single genus, while the last one takes in a somewhat wider range, extending from the lowest living member of one order to the culmination species of one line of the next higher order in the phylogenetic relationship.

THE GENUS LYCOPODIUM.

There are several phyletic lines in the living species of *Lycopodium*. Taking representatives of our common northern species from the simplest to the most complex, we obtain the following progressive series:

1, *Lycopodium lucidulum;* 2, *L. alopecuroides;* 3, *L. annotinum;* 4, *L. clavatum;* 5, *L. obscurum;* 6, *L. complanatum;* 7, *L. tristachyum.*

In the lowest species, *Lycopodium lucidulum*, there is no determinate reproductive axis, the zones of sporophylls simply alternating with the zones of foliage leaves. There is no difference in the response of the various buds, all growing in one direction against the force of gravity and the direction of light. There is practically no dimorphism of the leaves and the leaves have practically no phototropic reaction, not being

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able to adjust themselves even out of the shade of their own stems. The growth of the stem is comparatively slow and about the same in all the buds. The dichotomous division of the buds is also comparatively slow. As one goes upward through the series of species there is almost a uniformly progressive building up of a more complex reaction system. Each new acquisition is carried through to the end of the series and is often decidedly improved. In *Lycopodium alopecuroides* a determinate condition is established with the reproductive process, which gives rise to a poorly differentiated cone. There is also some slight difference between sporophylls and leaves. A differentiated growth potentiality is introduced so that one branch of a dichotomy grows faster than the other. The slow-growing branch is the determinate reproductive branch which grows erect while the second branch of the dichotomy is a more rapidly growing, more flexible vegetative and indeterminate branch. Although the vegetative branch grows upwards it is finally brought to the ground because of its flexibility and takes root at the point of contact from which the growth and reaction continue as before.

In *Lycopodium annotinum* the differentiation between the branches of the primary dichotomies is far advanced. One branch is creeping, grows rapidly at right angles to gravity and the substratum while the other grows erect and often divides several times. All the axes of the erect branches show a definite determinate growth, some ending in cones and some stopping growth permanently in the vegetative condition, while the horizontal branch grows indefinitely. There is a very decided dimorphism between the sporophyll and foliage leaf but no peduncle is developed, the transition being directly from foliage leaf to sporophyll at the base of the cone. Thus three great properties are established which are characteristic of most of the highest plants, namely, reproductive and vegetative determinate axes and differentiation of foliage leaves and sporophylls.

In the fourth stage, represented by *Lycopodium clavatum*, efficiency of the growing system of the creeping branch is increased decidedly and the erect reproductive shoot becomes more of a unit. But the greatest advance is a disturbance established between the vegetative part and the cone, a very prominent peduncle being produced with highly specialized reduced leaves. This peduncle usually divides once giving

rise to the most primitive type of inflorescence, a cluster with two flowers. The disturbance between the flower and the vegetative system below is a nearly universal characteristic of all higher plants. It is one of the important progressive movements and in *L. clavatum* we have one of its first appearances. The plant now has three distinct types of leaves without taking account of the specialization of the leaves on the creeping rhizome, due probably to a special environment in the surface of the substratum.

In *Lycopodium obscurum* (No. 5) the aerial branching system becomes much more complicated and the leaves on the determinate vegetative branches begin to show a decided reaction to light during their development. To a small extent also the branches show a definite reaction and are beginning to spread out into imperfect fan-shaped systems. In practically all lines, *L. obscurum* is an advance over *L. clavatum* except that it has not evolved a peduncle. Occasionally even in a very definite orthogenetic series a certain member may retain a primitive condition while most of its other important characters are evolving in a regular forward progression.

All of the progressive movements and complexities so far established in the series are carried forward in *Lycopodium complanatum*. The rhizome is very long and has a rapid growth; the branching system of the erect stem is decidedly more complex; and the dichotomy in the peduncle is increased so that each peduncle usually bears from four to eight cones. The determinate vegetative branches are decidedly flattened and dorsiventral with differentiated upper and lower surfaces and form definite fan-shaped systems spread out to the light because of the acquirement of a complex reaction, responding to light and gravity in a definitely correlated manner. The leaves on the flat branchlets are of three types; the two lateral rows are broad and alike, while the upper and lower rows are narrow and also differ from each other. This development of flattened fan-like systems of branches is repeated many times and becomes especially prominent in certain groups of conifers. Species with fan-like branches are especially abundant in *Selaginella* and *Thuja*. The progression in the reaction system to gravity and light and also in the morphological expression is very evident in this series. In *L. lucidulum* there is but one reaction for all buds; in *L. alopecuroides* there are two reactions but they are not very perfectly differentiated;

in *L. annotinum* there are two definite reactions; in *L. obscurum* there are three; and in *L. complanatum* there are also three reactions, but they are more complete or extreme than in *L. obscurum*.

Lycopodium tristachyum is a little more extremely developed along the same lines as *L. complanatum*, except that the branchlets appear less flattened because they are narrower and the leaves more reduced. There is greater branching potentiality in the aerial shoots so the peduncles commonly have 8 or more cones instead of 4–6. The vegetative branches composing the fans are also more numerous and the horizontal stems are extensively creeping, 1–4 in. below the surface. There are seven distinct types of leaves on the plant the same as on *L. complanatum*.

Lycopodium complanatum and *L. tristachyum* compared with *L. lucidulum* show, among other characters which might be considered, the following ten important lines of cumulative, evolutionary advancement:

1. From indeterminate growth for all axes to determinate growth of the reproductive branches in addition to the indeterminate growth of the creeping axis.
2. From no definite dimorphism of the foliage leaves and sporophylls to a decided dimorphism with highly differentiated sporophylls.
3. The origin of definite determinate growth in the vegetative aerial branches.
4. Evolution to a dorsiventral shoot system, involving leaves and stems and giving a definite reaction to light, the upper side being darker green than the lower side.
5. Differentiation of the leaves has taken place, so that, counting the sporophylls, there are seven distinct types of leaves instead of the uniform type of *L. lucidulum*.
6. Development of a very rapidly growing and extensive rhizome.
7. Differentiation of response to gravity and light has been introduced so that at each primary dichotomy of the indeterminate horizontal axis one of the twin buds grows at right angles to the force of gravity and the other grows upward against it.
8. Development of a branching system in the reproductive shoot giving rise to an inflorescence.
9. Development of a peculiar type of hereditary expression between the flower and the vegetative axis below, giving rise to a prominent peduncle.
10. Great development and improvement in the vegetative branching system through the presence of a more rapid dichotomy of the growing bud of the aerial shoot.

The development of flowers, differentiated sporophylls, peduncles, and inflorescences, through branching activity expressed in the reproductive shoot, are all decidedly characteristic of the higher plants. The change from a simple vegetative geotropic response to a complex reaction to gravity of various vegetative points of the stem system is also repeated in a multitude of cases in the higher plants. The reaction is to a condition universally possible to all and since only a part took the step, the cause is not to be looked for in the presence of the ground environment beneath nor to the influence of gravity, which acts equally all over the earth, but in the ultimate constitution of the structure of the living systems involved.

THE GENUS EQUISETUM.

The genus *Equisetum* represents a survival of a single small group of a phylum that in ancient geological times had an abundant and complex development. *Equisetum* is both primitive and at the same time highly specialized. The living species form a system of quite closely related groups which show a remarkably consistent progression from the lowest stage to the very highest. Disregarding the segregative characters and various repetitions which appear at the culmination points of the six main sections into which the genus falls, the complete progressive accumulation of the important characters can be represented by the following series:

1, *Equisetum giganteum;* 2, *E. myriochaetum;* 3, *E. ramosissimum;* 4, *E. laevigatum;* 5, *E. fluviatile;* 6, *E. silvaticum;* 7, *E. arvense.*

Equisetum giganteum is a plant with a long-lived aerial shoot with numerous whorls of branches, with a large, sessile, apiculate, green terminal cone and with numerous small cones on the branches. The ring or calyx at the base of the cone bears sporangia on the upper side. The plant is said to attain a length of 20 ft. or more. In *E. myriochaetum* there is a considerable reduction in size but there are still abundant whorls of branches. *E. ramosissimum* is still more reduced and the branch whorls are rather sporadic. In *E. laevigatum* the branches are very sporadic and often entirely absent. The next species on the list, *E. fluviatile*, belongs to a different line and connects more closely with *E. giganteum* but is in most respects on a much higher level than *E. laevigatum*. *E. fluviatile*

has whorls of branches and bands of stomata like *E. giganteum*. It has advanced very decidedly from the primitive condition represented by *E. giganteum*. The aerial stem is annual instead of perennial, the cone is without a point because of a more prompt determination of the floral axis, the calyx is usually entirely sterile, and there is a rather definite beginning of the evolution of a peduncle. The fertile and sterile shoots show no dimorphism except that the one has a cone and the other has none. In *E. silvaticum*, aside from its specific specializations, there are several important advances. The fertile and sterile shoots are decidedly dimorphic. The fertile shoot has little chlorophyll at first and no whorls of branches and the peduncle is quite prominent. Later whorls of green branches develop on the fertile stem and only the cone and its peduncle wither after the spores are shed. The cones are differentiated underground at an early stage and not delayed until after the aerial stems have developed as in the preceding species. In *E. arvense* the progression is carried to the extreme. The fertile and sterile shoots are decidedly dimorphic. The fertile shoot develops no branches and has little or no chlorophyll. The differentiation of the flower is begun underground at the inception of the shoot during the previous season. The entire fertile stem withers in a few days after it comes out of the ground when the spores are shed. The peduncle is very highly developed and the whorl branches are solid and have but three or four ridges on the internodes.

It is a remarkable fact that in so far as the morphology has been worked out the evolution of the gametophyte moves forward consistently in the same general direction. The gametophytes are comparatively large in *E. laevigatum* and *E. debile* and are hermaphroditic while in *E. arvense* they are comparatively small and are normally unisexual. In the hermaphroditic species the archegonia are devloped first and later the antheridia. There are sometimes as many as 200 archegonia on a single hermaphroditic plant. The embryology also indicates that the first four species of the given series are the more primitive and nearer the eusporangiate ferns than the last three.

Comparing the sporophytes of the last species with the first, we note the following additions to the hereditary potentialities which represent the progressive evolutionary movements that

have taken place to bring *E. arvense* to its high level of complexity:

1. The aerial shoot evolves from the perennial to the annual condition. This same movement appears in two other lines of Equisetum and has taken place in large numbers of the higher groups of plants.
2. The fertile shoot changes from an abundantly branched condition to a specialized stem without branches.
3. The fertile shoot including the flower, has lost nearly all of its chlorophyll and is brown in color. This loss of chlorophyll is a general evolutionary movement in all the higher flowers.
4. The fertile shoot evolves from a long-lived system to a very short-lived system, withering soon after emerging from the ground.
5. The fertile shoot is developed entirely underground, complete for spore dispersal and differentiated from the beginning.
6. The cones are more definitely determinate and do not have a vegetative point. This progression toward greater promptness in determination of the reproductive axis is a universal trend in all the higher plants.
7. There is a distinct reduction in the number of sporophylls because of the earlier determination and this movement is also practically universal in floral evolution.
8. The calyx evolves from a sporangium-bearing whorl to a completely sterile structure, thus giving a definite, sterile perianth, the first to appear among the living species of vascular plants.
9. A prominent peduncle has evolved below the flower, duplicating the corresponding evolutionary movement in *Lycopodium*. The peduncle is very generally evolved in the plants above this level.
10. The fluctuation between flower and vegetative tip with the development of intermediate semi-sterile cones is quite rare while in the species on a lower level it is exceedingly common. In the higher flowering plants intermediate shoots are exceedingly rare, in fact practically non-existent.
11. The fluctuation in the length of the vegetative internodes is less common than in the lower species.
12. The aerial shoots are very much smaller and this movement is prominent in every section of the genus.
13. Proliferation, which represents a return of the reproductive axis to the most primitive condition is much less common than in species on a lower level belonging to the same general group, like *E. fluviatile* for example. The same condition holds for low types of flowers in higher subkingdoms. Proliferation is common in such genera as *Araucaria*, *Larix*, and *Rosa*, while it is absent or exceedingly rare in the highest.
14. The number of teeth and sheath segments of the branches is very definite in *E. arvense*, being three or four, while in the lower species the numbers fluctuate decidedly.
15. Cones are rarely developed on branches, even in related species where branch whorls are still present on the fertile shoots, while in *E. giganteum* and other low species branch cones are a regular feature.

THE GENUS SMILAX.

Smilax represents one of the very extremely specialized groups of the monocotyls. The greenbrier family is plainly closely related to the Convallariatæ as represented by *Polygonatum*. In fact, Smilax is apparently only a specialized branch of the same phylogenetic series. The main series of progression is well represented by the following species:

1, *Polygonatum commutatum;* 2, *Smilax ecirrhata;* 3, *S. herbacea;* 4, *S. pumila;* 5, *S. glauca;* 6, *S. hispida;* 7, *S. lanceolata.*

Polygonatum commutatum has a creeping, more or less fleshy rhizome with an annual aerial herbaceous shoot usually from 3–6 feet high with about 20 leaves, the internodes being about 1–1½ in. long except the basal one which is often 16 in. or more in length. It has bisporangiate flowers and the anthers have four microsporangia. There are no tendrils. In most other general characters it is much like an herbaceous *Smilax*. Both in *Polygonatum* and *Smilax* there are two-ranked leaves which condition is a very general culmination in the monocotyls in the evolution from a three-spiral condition. In the lowest species of *Smilax*, namely, *S. ecirrhata*, the two-ranked condition is not very definite.

Now in passing from *Polygonatum commutatum* to *Smilax ecirrhata* four very important progressive changes are in evidence. The plants become diecious, the microsporangia are reduced to two in the anther, there is a slight development of woodiness in the lower part of the plant, brought about by the hardening of the pith, and a potentiality is added for developing tendrils on the petioles. The new tendril heredity is only active toward the end of the ontogeny of the aerial shoot. The tendril potentiality has been added to the previous normal leaf heredity. The old potentiality is not destroyed, but is active in the juvenile condition. The new tendril heredity is latent until the juvenile physiological gradient is passed, when the functional conditions of maturity throw it into play. In this case, therefore, there is recapitulation of the ancestral character at the beginning of the ontogeny. Very frequently the new heredity added to a system is such that it becomes active in the juvenile condition and recapitulation may then occur at the end of the ontogeny or even in the middle stage. In *S. ecirrhata*, if the plants are small, so that growth does not

continue long enough, there will be no tendrils whatever even on the last leaves.

Passing over to *Smilax herbacea*, we have the same general type of plant although the tendrils usually appear somewhat earlier. The first tendrils usually appear on the 5th to 10th leaf. All the subsequent leaves will have tendrils normally. A new factor is now introduced which is destined when fully evolved to produce a most remarkable monocotyl. This is a potentiality for rapid and prolonged growth. This new potentiality causes the mature plant to elongate rapidly and thus a viny stem is developed which, because of the presence of tendrils on the leaves gives the plant a slight climbing ability. It will be noted that the tendrils were evolved in a plant which has no climbing ability otherwise. *S. herbacea* is somewhat less woody than *S. ecirrhata*.

In *Smilax pumila* the rambling factor is considerably augmented and the stem which is still terete is weak or reclining and still only about 2–6 ft. long. The woodiness of the stem is not very marked, but is nevertheless much more prominent than in the preceding species. As intimated above, the woodiness in all the species of *Smilax* is a new characteristic and is produced by the hardening of the walls of the ground tissue or pith and not by an increase of xylem in the vascular bundles. It is entirely a secondary evolutionary acquisition laid down on top of the original potentiality responsible for ordinary pith parenchyma. The petioles and tendrils of *S. pumila* are also not very woody. All of the four species considered so far have prominently elongated basal internodes, usually the first two above ground. The lowest internode is usually from 4–12 in. long and the second from 3–6 in. The internodes between the foliage leaves usually range as follows: *Polygonatum commutatum*, 1–1½ in.; *Smilax ecirrhata*, 1–2 in.; *S. herbacea*, 1–3 in.; *S. pumila*, 1–4 in.

In passing up to number 5, *Smilax glauca*, we meet the first typical greenbrier. The stem is completely woody and the woodiness extends to the petiole base and tendrils. The leaf blade is deciduous beyond this woody base. The internodes are perceptibly longer on the main axis than in the preceding species, usually being from 2½–4 in. long. The rhizome is long and slender and prickly but somewhat tuberous. The tendrils appear earlier in the ontogeny, usually on the fourth to sixth leaf. The stem has prickles which is a new evolution and

these are present on most woody species. The stems are usually about 6 to 12 ft. long and definitely climbing, but still inclined to be somewhat bushy. The rambling habit is far from being completely evolved. The ultimate twigs are definitely quadrangular. Many of the woody species have these quadrangular twigs not because of any advantage or disadvantage, for similar quadrangular twigs appear in many monocotyls and dicotyls, in herbs as well as woody plants, in aquatics as well as in ordinary aerial mesophytes. The quadrangular character is frequently associated with the attainment of the two-ranked condition or opposite leaves. It represents an evolutionary progression from a radially symmetrical system to a bilateral system. Ornamental white spots are usually in evidence on the leaves of *S. glauca*. There is also a progressive reduction of the ovulary in the series. *Polygonatum* has several ovules (6–2) in each cavity; in the herbaceous species of *Smilax* there are two ovules in each cavity; while in the higher group, or woody species, there is but one ovule in each cavity. Thus the ovulary is approaching the ultimate unilocular condition.

The next evolutionary step gives a typical greenbrier in *Smilax hispida*. The rapid growth factor is greatly increased so that this liana frequently climbs up in trees 30 to 45 ft.; the internodes of the main stem are commonly 4–10 in. long. The stems are usually also very prickly. In general the progression toward an ideal liana is far advanced.

Taking *Smilax lanceolata*, or Florida Smilax, as an ideally developed liana species, several prominent orthogenetic advances are in evidence. The plant grows at an enormously rapid rate and the internodes are frequently over 1 ft. long. The plant often climbs up 70 to 80 ft. to the top of tall trees, and has scattered prickles on the main stem, although none on the branchlets. Only the first or second leaves are usually without tendrils. The tendrils appear in successively earlier stages of the ontogeny as one passes through the *Smilax* series. The leaves are usually decidedly narrowed and have only 3–5 nerves (mostly 3) instead of the 15–21 nerves present in *Polygonatum* or the 5–13 nerves present in the species from Nos. 2–6. The leaves have become persistent, which might, of course, be a condition handed down from the ancestral type in the series. In the closely related *S. laurifolia*, the fruit ripens only the second year. The underground system consists of large tuberous stems suggesting very large potatoes. These

tubers also represent the extreme when compared with the preceding species, beginning with the creeping rhizomes of *Polygonatum*.

When one considers carefully the changes which take place step by step in this series of seven species, he discovers a most remarkable building up process which shows how evolution progresses by the addition of new character potentialities on top of the old and by the orthogenetic perfection of the characters when they are once added. All of these plants are dwellers in the forest and thicket. The series is not to be explained on any assumption of impelling environments nor by any notions of special utility, although a Lamarckian might here actually find a special utility in the base of the petiole and the tendrils. But as is evident from the analysis given above, the tendrils and woodiness began to appear before there was any use for them and the beginning of the stretch habit appeared before there was any real climbing to be done. As to the leaf forming the abscission at the outer end of the petiole instead of at the base, which might seem like a plain case of survival through advantage to a believer in Darwinism, the same thing occurs in species of *Rubus* and other plants where no tendrils are present and where no stem is to be held up to a support. The teleological explanation of quadrangular twigs, prickly stems, fruit delaying its maturity to the second year, and especially the prickles on the underground rhizomes should certainly strain the credulity of even the most credulous to the breaking point.

THE GENUS VIOLA.

The violets show a very beautiful orthogenetic movement from the bottom to the top of the series. The following species will represent the main progression:

1, *Crocanthemum canadense;* 2, *Cubelium concolor;* 3, *Viola canadensis;* 4, *V. odorata;* 5, *V. pallens;* 6, *V. papilionacea;* 7, *V. palmata;* 8, *V. pedatifida.*

The ancestral type of the violet family may in a general way be represented by *Crocanthemum canadense* which has erect stems, sometimes 2 ft. high, short-petioled leaves, only slightly zygomorphic flowers, and numerous stamens. It has both showy petaliferous flowers and apetalous cleistogamous ones. The cleistogamous flowers are, of course, a specialization which might not be present in the lower violets.

In *Cubelium concolor* the more typical violet characters are already evolved. Although the stem is still erect with short-petioled leaves and short-peduncled flowers, the flowers are decidedly zygomorphic and the stamens are reduced to five.

In *Viola canadensis* the generic characters of *Viola* have been fully attained and the sepals are highly specialized, being more or less prolonged posteriorly. This character is still missing in *Cubelium*. The two lower stamens are also specialized, being distinctly spurred. The flowers are thus much more zygomorphic both externally and internally. Two other very characteristic violet characters are evolved to a moderate degree. Although the plant still has an erect aerial stem, the petioles and peduncles show a distinct tendency to elongate. This movement will end in a very extreme condition in the higher geophilous violets. It is to be noted again that the evolutionary movement begins before there is any need of it and before the plants show any definite tendency toward geophily. In this species petaliferous flowers are still often produced throughout the summer.

The group of violets to which *Viola odorata* belongs shows a strong movement toward the development of the geophilous condition in that there are long and slender leafy stolons produced above ground. The most remarkable potentiality added is the dimorphic production of flowers. This plant as well as most of the species on a higher level in the same phyletic series has both the ordinary showy flowers and apetalous cleistogamous flowers which have only two functional stamens.

In *Viola pallens* the orthogenetic movement has advanced further and the plant has long slender rhizomes and in addition slender creeping stolons.

Viola papilionacea represents a typical blue violet. The stem has become a thick, fleshy rhizome without aerial runners; the petioles and peduncles of the showy flowers are exceedingly long while the peduncles of the cleistogamous flowers are rather short; the showy flowers are decidedly zygomorphic, with three distinct types of petals.

In *Viola palmata* the rhizome is more extreme and the leaves are palmately 5–11-lobed, while in *V. pedatifida* the extreme of the series is reached in a plant with short erect rhizomes and palmately multifid leaves with very narrow segments.

The evolution of cleistogamous flowers in a series which has only showy insect pollinated flowers at the lower levels shows how incorrect the older hypotheses of evolution, like use and disuse and natural selection, were; for these higher violets all produce showy flowers which are extensively visited by insects but which produce little or no seed. During the summer period the cleistogamous flowers are developed in great abundance and on the same individuals and produce large quantities of seed from which the species is abundantly propagated. This development of cleistogamous and sometimes parthenogenetic flowers at the ends of many evolutionary series of Anthophyta of both entomophilous and anemophilous plants plainly indicates that the libraries of books and articles written to prove that the showiness of the flower was evolved to attract insects to insure cross pollination are to be considered largely in the same light as our mother goose fairy-stories. Nectar glands and fragrant odors are associated with some sporophylls of ferns long before there were any flowers and before there was any pollen to be carried, and attractiveness of beautiful colors and even zygomorphy are frequently in evidence in the lower wind pollinated series, while many of the entomophilous series end in exceedingly inconspicuous types.

A CONIFER SERIES.

There are many exceedingly interesting progressive series in the Coniferæ. The following one will illustrate a progressive building up of a very complex hereditary system from a comparatively simple one, the series running through two families and a number of genera.

1, *Araucaria imbricata;* 2, *Cunninghamia sinensis;* 3, *Sequoia sempervirens;* 4, *Pseudotsuga mucronata;* 5, *Picea abies;* 6, *Cedrus lebani;* 7, *Pinus strobus;* 8, *Pinus serotina;* 9, *Pinus radiata;* 10, *Pinus muricata.*

Araucaria imbricata is a very primitive type of conifer. It has a rhythmical development of branches on the main stem and the foliage leaves are close-set in spirals. The leaves of the main stem have no developed buds in their axils except at certain intervals and are all of the same general type. There are no bud-scale leaves, the resting period being simply marked off by a zone of shorter, smaller green leaves. The leaves have no phototropic ability. The whorl branches also have

sporadic development of buds in the leaf axils and these develop into prominent secondary branches which are a sort of dwarf branch. There are no internodes on the plant. The staminate and carpellate cones terminate leafy branches and the sporophylls are very leaf-like.

In passing up to *Cunninghamia sinensis* there is evident a considerable narrowing of the leaves and the leaves also show a phototropic reaction. There is a slight beginning of a resting bud with specialized bud scales. The staminate cones are in clusters and the carpellate cones also show a tendency to be clustered although they are often solitary at the end of a leafy shoot. There is a considerable difference between sporophylls, and foliage leaves. The carpels, however, still show a distinct midrib and other leaf characters.

Sequoia sempervirens shows an increase in the evolution of the resting bud and bud scales. The leaves are linear and react definitely to light and the carpels are highly specialized and thickened. These three species form a suitable, primitive background for the pine series proper.

In *Pseudotsuga mucronata* the winter bud is well evolved and shows dry scale leaves. The carpels have large carpellate bracts and the thickening takes place in a different manner from that in *Sequoia*, the lower part of the carpel back of the seeds being developed into a distinct structure, the ovuliferous scale. The tree, therefore, has four distinct kinds of leaves, instead of three as in *Araucaria imbricata*. The foliage leaves are linear, being evolved to the same condition as in *Sequoia sempervirens*. *Pseudotsuga* along with the remaining genera of Pinaceæ has winged pollen in contrast to the lower Taxodiaceæ and Araucariales.

In *Picea abies* the leaves have become prismatic but still show a slight reaction to light in bending away from under the twig. The carpellate bracts have been reduced and are hidden beneath the ovuliferous scales which are much as in *Pseudotsuga mucronata*. There are sporadic buds which develop into small branches in numerous leaf axils between the main branch whorls and the branches also show sporadic bud and branch development in some leaf axils. The plant is thus definitely evolving to a less simple, less symmetrical system.

Cedrus lebani shows a considerable evolutionary advance in the acquisition of sporadic dwarf branches which, however, have indefinite growth. The foliage leaves on the dwarf branches are

beginning to elongate and are in the first stages of the evolution of needle leaves. The scale leaves of the dwarf branches are somewhat different from those of the long branches. The leaves of the long branches are also different from the foliage leaves of the dwarf branches. The ovuliferous scales, although of the same general type as in *Pseudotsuga* and *Picea*, are more thickened and woody. The cedar thus has two kinds of foliage leaves, two kinds of bud scale leaves and two kinds of sporophylls.

Now, passing over to the genus Pinus, several important new characters are again added. In *Pinus strobus* the ovuliferous scale shows three new characteristics which are not present in *Pseudotsuga*. The scale is elongated, is showing considerable woodiness and has a peculiar ornamental tip. The leaves on the main axis and long branches are changed to dry scales and each one develops a bud which gives rise to a dwarf branch. These dwarf branches are determinate in growth and after developing bud scale leaves and five foliage leaves are completely arrested in further development. Thus vegetative determinateness is again evolved. After several years each dwarf branch is self-pruned by the development of an abscission layer. The foliage leaves are longer and more definitely needles than in the cedars and larches. The white pine, therefore, has developed an enormous efficiency for producing axillary buds when compared with *Araucaria* or *Cunninghamia*. In the next higher family beyond the pines, the Juniperaceæ, as for example *Juniperus barbadensis*, the number of buds and twigs in a comparable branch system is again enormously increased when compared with *Pinus* although bud development is sporadic and many leaf axils do not produce functional buds. *Pinus* has four kinds of mature vegetative leaves besides the two kinds of sporophylls or twice as many general types as *Araucaria imbricata*. In addition there is still a seventh kind of leaves present in the system, the special juvenile leaves of the seedling to say nothing of a distinct kind of cotyledons. The basal elongation of the needle leaves becomes very pronounced in some species of pines. In the white pine there is a peduncle on the subterminal carpellate cones, but this is a specialization which is not continued in the yellow pine group, represented by the last three species of the series given, although these have a very marked modification of the lower carpels. The cones ripen promptly in the summer of

the second season. The pollen, of course, has the highly specialized two wings or sack-like appendages.

Pinus serotina shows a decided specialization in developing "wrapper" scale leaves on the dwarf branches. The foliage leaves are reduced to three on the dwarf branch and are more extremely evolved as elongated, rigid needle-leaves. The ovuliferous scales are more elongated, much more woody, and have a much more extreme, ornamental apex than in *Pinus strobus*. The cones are lateral showing the beginning of irregular branch development as in *Picea*. There is also a very decided shortening of the base of the carpellate floral axis, giving rise to a wide sterile zone of carpels. This is again a first step in the evolution of a perianth. The terminal carpels also show a different development. Thus there are three general types of carpels and three rather distinct regions of the cone to be definitely recognized. These differences are less pronounced in the lower members of the series.

In *Pinus radiata* a striking new property is added, resulting in a decided zygomorphy of the carpellate cone. Zygomorphy is a characteristic of nearly all the highest types of flowers of the Anthophyta. The ovuliferous scales are much larger on the outer side than on the inner and the tips have prominent rounded protuberances. Thus there are really four general types of carpels which, of course, intergrade with each other. With the five kinds of vegetative leaves and counting but one type of stamens, this pine has ten kinds of leaves besides the cotyledons. This certainly indicates a decided evolutionary advance in complexity when compared with the three types present in *Araucaria imbricata*, the two types in some of the higher ferns, or the single type present in many of the lower ferns, where no morphological difference is to be observed between sporophyll and foliage leaf except the presence of sporangia on the former.

Pinus muricata has much the same general characteristics as *P. radiata* but the ovuliferous scales are more elaborated. The knob below the apex is flattened and armed with a stiff flattened spine. The cones are decidedly zygomorphic as in *P. radiata*. There are but two leaves on the dwarf branches, which is the usual limit to determinateness in the higher pines except in one species of nut pine in which there is mostly but a single leaf on a dwarf branch. The higher pines are commonly characterized by irregular development of their crowns. This

is especially due to the intercalary development of long branches between the rhythmical branch whorls. In some species, as for example *Pinus contorta*, the old crowns are sometimes grotesquely irregular in contrast to the regular rhythmical symmetry of the lower white pines or the remarkable, repetitive symmetry of an araucarian.

In a tree fern there is normally but one terminal bud which gives a single type of morphological reaction; in *Araucaria imbricata* there are four kinds of stem bud reactions, the terminal bud, the primary and secondary branch buds, the carpellate cone bud, and the staminate cone bud. There is very little difference in the reaction of the main stem bud and the branch buds, but the former differentiates a radially symmetrical branch system while the latter differentiates a more or less dorsivential sytem which becomes extremely fixed so that when grown as a cutting it gives rise to an unsymmetrical tree. In *Pseudotsuga* there is the same general difference of four types of bud reaction, but the difference between the terminal stem bud reaction and the lateral twig is very much greater. In *Pinus* there are in general five types of stem bud reactions, the terminal stem bud, the main and lateral branch buds, the dwarf branch buds, the carpellate cone bud, and the staminate cone bud. Thus the genus *Pinus* again shows an extremely complex reaction system in its buds and plainly stands at the end of its phyletic series in this respect also.

It is truly astonishing that in this conifer series not only the general external organography and morphology show this orthogenetic accumulation of a more and more complex hereditary system but that there are several lines of minute characteristics which went through a closely parallel movement at the same time and in the same direction. Thus the lower gymnosperms, like *Cycas* and *Ginkgo*, have two cotyledons and the same number is present in *Araucaria*, in *Cunninghamia*, and in *Sequoia sempervirens*, while in *Sequoia washingtoniana* there are three to six and in the various species of *Pinus* the number range from five to fifteen. Thus the complexity of cotyledon development has kept step with the evolution of the general complexity of the pines. In the lower Ptenophyta which presumably represent the mother phylum of the Strobilophyta there is a single embryonic leaf. The parallel series or order of Taxales also evolved polycotyledony but not to so extreme a condition as the Pinales. This development of many coty-

ledons is a derived condition involving the determination of correlation centers in the ring of tissue surrounding the terminal bud of the embryo. There is much variation in the definiteness of the interaction and often two centers of activity do not become developed sufficiently for independent action, thus giving rise to twin cotyledons or in some cases apparently enlarged simple cotyledons with double vascular strands. Such phenomena are, of course, common in other similar structures, as the very common development of double or broad sporophylls in *Equisetum*. The development of double cotyledons and cotyledonary tubes has given rise to controversies and the development of a contrary hypothesis that the polycotyledonary condition was the original and the dicotyledonary one the derived condition. But this would go counter to all the complex progressive movements and is not to be taken seriously. There is no basis for turning evolution topsy-turvy because of a fantastic method of interpretation of abnormalities.

In Cycas and *Ginkgo* a single embryo is organized from the egg, which is the usual condition from the liverworts on up. In *Araucaria* there is also a simple embryo without a rosette at the basal end beyond the suspensor. Passing up to the Pinaceæ one finds a decided and progressive advancement toward the most extreme condition. In *Pseudotsuga* a single embryo develops from the egg and a long suspensor but apparently no rosette cells. In *Picea* and *Abies* a single embryo is developed with rosette cells beyond the base of the long suspensor cells and essentially the same condition exists in *Larix* which in general morphology represents a more advanced condition. But in *Tsuga* a new condition is introduced and the condition of cleavage polyembryony is established, four embryos developing from a single egg. *Cedrus* which in some respects is on a lower stage of evolution than *Larix* has advanced its embryogeny to the extreme condition approaching that of the pine. There is not only cleavage polyembryony but rosette embryos are also produced. The culmination of the embryonic complexity of the Pinaceæ is reached in the genus *Pinus* where the egg, through cleavage polyembryony, develops four incipient embryos at the outer end of the long suspensor and four prominent rosette embryos at the basal end. In Biota cleavage polyembryony is even much more extreme than in the pines. Thus it is seen that the embryonic evolution moves in complete

harmony in the same direction and in general keeps pace with a large number of progressive characters, thus giving rise to the exceedingly complex reaction systems present in the highest pines.

The advancement in simple bilaterality of the sporophylls is also plainly in evidence in this series. In *Araucaria* there is one central seed, in *Cunninghamia* three, in *Sequoia* four to nine, while in some of the more specialized genera of Taxodiaceæ and in the Pinaceæ the number is uniformly two, evenly balanced on the two sides of the carpel.

Another interesting development is shown by the time of maturing of the carpellate cones. Primitive forms apparently all matured their cones in a single season as is the case in *Cycas*, *Pseudotsuga*, *Picea* and *Tsuga*. In *Larix* the fruiting cones also mature the first year while in *Pinus*, the culmination of the series, the cones do not ripen until the second year. In *Juniperus*, belonging to a higher related series, some species mature their cones the first year and some the second.

The progressive reduction of the male gametophyte in the conifers also parallels the other general movements. In *Araucaria*, the pollengrain shows its primitive character by developing from 20 to 44 vegetative thallus cells (prothallial cells) besides the spermatogenous, stalk, and tube cells. In *Pinus*, which stands at the top of the Pinaceæ and far above the Araucariaceæ in nearly all characteristics, two minute and evanescent vegetative thallus cells and finally spermatogenous, stalk, and tube are produced. In the Juniperaceæ, the extreme group of the Pinales, no vegetative thallus cells whatever are developed and the pollengrain usually contains only two cells. The Taxales show a higher level in male gametophyte reduction at the base than the Araucariales, as would be expected. In some species of *Podocarpus* as many as 8 vegetative thallus cells may be developed in the pollengrain, and in various other species and related genera there is a reduction, until the highest condition is attained in the Taxaceæ, where no vegetative thallus cells are produced, just as in the Juniperaceæ, but the first division gives rise directly to the spermatogenous and tube nuclei. These plants are in this respect on the same level of advancement as most of the Angiospermæ. It is remarkable that just as in the Pinales, the extreme reduction of the male gametophyte is in the Taxales also correlated with other extreme evolutionary morphological developments. The

reduction of the male gametophyte is thus consistently orthogenetic in a most remarkable manner.

A study of the wood in the series also shows a remarkably consistent progression. The cycads have a multiseriate condition of the bordered pits on the tracheids and the pits are somewhat elongated. This is evidently the primitive condition for living gymnosperms. In *Araucaria* there are also two or more rows of bordered pits usually present on the radial walls of the tracheids while in *Cunninghamia* there is mostly a single row. This specialization is carried through to the highest pines and the bordered pits become very circular instead of showing the elongated condition common in *Cycas*.

In *Pseudotsuga* the wood contains a number of characteristics which indicate a lower condition than that shown in *Pinus*. In *Pinus strobus* the upper and lower walls of the few and small ray tracheids are smooth and have the radial walls of each ray parenchyma cell communicating by one or two large simple pits with each adjacent wood tracheid. In the yellow pines generally, like *Pinus muricata* or *P. virginiana*, a much more complex reaction system is in evidence. The upper and lower walls of the small and numerous ray tracheids are sculptured with ornamental reticulations and the radial walls of each ray parenchyma cell has three to six rather small simple pits communicating with each adjacent wood tracheid. Thus the evolution of the wood elements is moving in harmony with numerous other orthogenetic progressions.

Finally another most remarkable parallel movement took place in relation to resin cells and resin passages. This series was worked out by Penhallow. Resin cells occur in the more primitive conifers and are scattered in the bast; in the next stage they occur in zones and finally they are definitely segregated. Segregated resin cells may give rise to resin cysts, as are present in *Sequoia*, *Tsuga*, and *Abies*. In *Pseudotsuga*, *Picea*, and *Larix*, the continuous system of resin canals are present and show their derivation from resin cysts by the constricted walls. In *Pinus* the walls are no longer constricted and are lined by a thin-walled epithelium, except in a few types where thick-walled cells are interspersed with the thin-walled ones. This series coincides very closely with the other numerous orthogenetic movements. Only *Pseudotsuga* seems to have marched ahead a little of its expected position in this respect. The series indicates again that the Pinaceæ are a

highly evolved type of conifers and that *Pinus* is the most specialized genus of the family.

In some genera of the Pinaceæ resin canals are absent from the woody tissues of the stem except in the first annual ring of vigorously growing shoots, as in *Abies*, or the resin canals may occur only traumatically. In these cases one may assume that in such a condition a new potentiality has been added which under normal conditions interferes with the expression of the character or, on the other hand, the potentiality for resin canals may have been added even after the primary phylum had been segregated into the secondary phyla as *Abies*, *Tsuga*, *Cedrus*, etc., and then never was able normally to come to expression because the inhibiting factor had been acquired previously.

When one considers all these remarkable orthogenetic movements running from *Araucaria* to *Pinus* in the same general direction, one begins to get some superficial notion of the wonderful process which was responsible for the taxonomic system as we find it in the world today. What was it that kept all of these movements marching step by step, with hardly a deviation, in a definite direction to the end? What kept the mutative processes of the hereditary potentialities in the straight and narrow path during the long course from the comparatively simple araucarians to the highly complex reaction systems of the higher yellow pines? The very thought of special utility suggests a childish question, the notion of teleological selection is quite preposterous, the idea of a direct response to environment is ridiculous. Such notions have no correspondence with the actuality. So we will finally have to get down to the study of the nature and structure of protoplasm, yes, even to a study of the dust of the earth from which it had its origin, if we are ever to even approach the immediate causes involved in the evolutionary process.

Now this inventory of the cumulative evolution of hereditary potentialities giving rise at each stage to more and more complex characters and reactions by the addition of new heredity to the old cannot be properly appreciated unless one actually studies the complete series containing the additions step by step. If this is done then one must obtain a firm conviction that the order of presentation given above is the true evolutionary order and represents the actual general trend of the evolving system. Such a study properly undertaken will

plainly show that evolution is cumulative and progressive, "precept upon precept, line upon line," potentiality upon potentiality. There is, in general, nothing hap-hazard about it. It pays no special attention to conditions and environments except in so far as the environment may or may not permit survival. In the series given all the numerous changes and additions have an equal survival value in many diverse habitats. The matter of survival is not involved at all in the characters discussed. Plants with practically none of the peculiarities are to be found prospering side by side with those that have the peculiarities. Take for example the evolution of winged pollen mentioned above. This has appeared independently in entirely different conifer lines, and conifer species with winged pollen and without thrive in the same forest. All the members of the evolved series were surrounded by the same air and subject to the same winds. The wings are not at all necessary for survival. On the other hand, they do no harm. Pollination is assured whether wings are present or not.

The whole evolutionary process, described in the five examples, presents the working out of a wonderful cosmos, a system unfolding according to some fundamental principle which we have not discovered scientifically but which is nevertheless clearly and inevitably at work in bringing out the remarkable succession of potentialities in a substance, the protoplasm, which must at the beginning have been an undifferentiated system with enormous possibilities.

The present studies show that evolution has forced its way through the circumstances of environment, ever leading forward, and that new complexities and new efficiencies have been added from time to time through an evolutionary creative principle in the same way that the creative human mind adds improvements, complexities and efficiencies to its machines and mechanical devices year by year and from age to age, until the perfect and the ideal are attained at the end, whether it be an automobile, a flying machine, a compound microscope, or a radio receiving instrument. And thus it is that when we compare a dandelion with a man we find that, because of a common forward progressive and accumulative movement they are as much alike in important potentialities which they have evolved in common as they are both profoundly different from one of the primitive members of the living kingdom, for example, a nonsexual, holophytic, unicellular bacterium.